

ORIGINAL ARTICLE

A remarkable new genus of Cretaceous dustywings (Neuroptera: Coniopterygidae) in amber from northern Myanmar

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Abstract A new dustywing genus and species, namely *Cretaconiopteryx grandis* **gen. & sp. nov.**, from the mid-Cretaceous amber of Myanmar is herein described in the lacewing family Coniopterygidae. The new genus is distinguished from all other dustywing species by the combination of following morphological features: relatively large body-size, comparatively rich crossvenation, origin of RP+MA near wing base in both fore- and hindwing, forewing RA and RP terminally fused into a loop, and proximally zig-zagged forewing CuP. A new subfamily, Cretaconiopteryginae **subfam. nov.**, is erected based on this spectacular new genus. The new subfamily might represent the basalmost lineage of known coniopterygids.

Key words Neuropterida, taxonomy, new species, Burmese amber, Mesozoic.

1 Introduction

Coniopterygidae (dustywings) are a distinctive family of Neuroptera owing to the minute body-size, the waxy covering, and reduced wing venation. They feed on small arthropods such as mites, aphids and scale insects. Currently, there are 571 described species throughout the world (Sziráki, 2011; Engel, 2016). Coniopterygidae have been considered to be a morphologically specialized family belonging to the paraphyletic Hemerobiiformia (Aspöck *et al.*, 2001; Haring & Aspöck, 2004; Aspöck & Aspöck, 2008; Zimmermann *et al.*, 2009; Randolph *et al.*, 2017), while recent studies based on multi-locus and genomic data suggest that this family is the sister group of the lineage comprising all other extant lacewing families and probably diverged during the late Permian (Winterton *et al.*, 2010; Misof *et al.*, 2014; Wang *et al.*, 2017). Coniopterygidae is composed of three subfamilies, i.e., Aleuropteryginae, Coniopteryginae and Brucheiserinae. The former two subfamilies are distributed worldwide and also known with many fossils from Mesozoic and Cenozoic periods (Engel, 2016), while the latter subfamily is restricted to southern South America and by far without any fossil records (Riek, 1975; Sziráki, 2007).

The oldest fossil record of Coniopterygidae refers to *Juraconiopteryx zherichini* Meinander, 1975, described based on an incomplete compression fossil from the Late Jurassic of Kazakhstan (Karatau). Almost all remaining fossils of the family are found in most major amber deposits of the Cretaceous and Tertiary periods (Grimaldi *et al.*, 2013; Engel, 2016) as follows: Lebanon (Hammana, Early Cretaceous, Neocomian: Whalley, 1980; Azar *et al.*, 2000; Nel *et al.*, 2005); Spain (Cantabria, Lower Cretaceous, Albion: Pérez-de la Fuente, 2012); France (Charente-Maritime, Lower Cretaceous, Albion: Nel *et al.*, 2005; Vendée, Upper Cretaceous, Cenomanian-Santonian: Perrichot *et al.*, 2014); Myanmar (Kachin, mid-Cretaceous, Albion-Cenomanian: Engel, 2004, 2016; Sziráki, 2016); U.S.A. (New Jersey, Upper Cretaceous, Turonian: Grimaldi, 2000; Engel, 2002); Russia (Taimyr Peninsula, Upper Cretaceous, Santonian: Meinander, 1975; Makarkin & Perkovsky, 2017); Canada (Alberta, Upper Cretaceous, Campanian: McKellar *et al.*, 2008); India (Gujarat, Eocene: Grimaldi *et al.*, 2013); France (Oise, Les Quesnoys, Eocene: Nel *et al.*, 2005); Baltic and the Ukraine (Eocene: Enderlein, 1910, 1930; Meinander,

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1975; Dobosz & Krzemiński, 2000; Kupryjanowicz & Makarkin, 2008; Engel, 2010); and the Dominican Republic (Miocene: Meinander, 1998; Engel & Grimaldi, 2007; Grimaldi *et al.*, 2013). The other fossil dustywings are known from the Pleistocene copal of Togo and Madagascar as well as the Oligocene of France (preserved as compression fossil) (Meunier, 1910a, b; Nel, 1990). Totally, there are 33 fossil and subfossil species in 21 genera (16 genera are extinct). Among these fossil dustywing genera, 13 genera belong to the subfamily Aleuropteryginae, while the remaining eight genera are attributed to the subfamily Coniopteryginae.

In this paper we report a new dustywing genus from the mid-Cretaceous amber of northern Myanmar where four genera and four species of Coniopterygidae have been recorded (Engel, 2004, 2016). Remarkably, the new genus greatly differs from all known dustywing genera by having the wing venation with more plesiomorphic characters besides a few notable derived features. The new genus is considered to represent a new subfamily. Morphological comparisons and discussion of the phylogenetic position of the new genus are presented.

2 Materials and methods

The Burmese amber samples under present study are from the Hukawng Valley in Tanai Township, Myitkyina District of Kachin State, Myanmar (see Kania *et al.*, 2015: fig. 1). The age of this deposit has been investigated and dated to be ~99 MA (earliest Cenomanian) by U-Pb dating of zircons from the volcanoclastic matrix of the amber (Shi *et al.*, 2012). The type specimen of the new species is currently housed in the Entomological Museum, China Agricultural University (CAU), Beijing, and they will eventually be deposited in the Collection of Xiao Jia in the Century Amber Museum (CAM), Shenzhen.

Photographs and drawings were taken and made using a Zeiss SteREO Discovery V12 stereo microscope system. The figures were prepared with Adobe Photoshop CS4®. Terminology of wing venation generally follows Aspöck *et al.* (1980). We did not use the terminology of wing venation in Meinander (1972) as it lacks homology with other lacewing families, although this wing venation system were frequently used in many papers on Coniopterygidae (e.g., Azar *et al.*, 2000; Engel, 2016). The presently used vein nomenclature is given below with comparison of that used by Meinander (1972) in corresponding parentheses. Terminology of genitalia follows Aspöck and Aspöck (2008).

Abbreviations used for wing veins are as following (Words in bracket were used in Meinander (1972)):

- A—anal vein;
- C—costa;
- Cu—cubitus;
- CuA (Cu₁)—cubitus anterior;
- CuP (Cu₂)—cubitus posterior;
- h—humeral veinlet;
- M—media;
- MA (R₄₊₅)—media anterior;
- MP (M)—media posterior;
- R—radius;
- RA (R₁ plus Sc₂)—radius anterior;
- RP (R₂₊₃)—radius posterior;
- ScP (Sc₁)—subcosta posterior.

3 Systematic palaeontology

Class Insecta Linnaeus, 1758

Order Neuroptera Linnaeus, 1758

Family Coniopterygidae Burmeister, 1839

Subfamily Cretaconiopteryginae subfam. nov.

Type genus: *Cretaconiopteryx* gen. nov.

Diagnosis. Head (Fig. 1F) longer than wide, with elongated gena; frons well-sclerotized between antennal insertions;

vertex feebly domed. Maxilla (Fig. 1F) with galea segmented. Both fore- and hindwing (Fig. 3) with relatively dense crossveins, some of which are arranged into a gradate series distally; costal space with several distinct subcostal veinlets on distal half; distal part of forewing RA curved posteriad and connected with anteriorly curved RP, forming a loop; RP+MA originated from R near wing base in both fore- and hind wing; three or four crossveins present between RP+MA and MP in forewing; forewing MP lacking stiff setae. Abdominal plicatures present at least on segments 3–4 (Fig. 2B).

Remarks. The new subfamily is herein erected based on the new genus, *Cretaconiopteryx* **gen. nov.**, which greatly differs from all other dustywing genera and cannot be placed into any of the three known subfamilies. Putative autapomorphies of Cretaconiopteryginae consist of the forewing RA and RP distally forming a loop, and the zig-zagged forewing CuP although these characters might also be autapomorphies just for the genus or even species (See Remarks of the new genus and Discussion). Moreover, the rather proximal origin of RP+MA in both fore- and hindwing as well as the gradate-like arrangement of crossveins are characteristic of this subfamily.

***Cretaconiopteryx* gen. nov.** (Figs 1–3)

Type species: *Cretaconiopteryx grandis* **sp. nov.**

Diagnosis. Large-sized dustywing (forewing length 6.67 mm). Antenna 27-segmented (with 25 flagellomeres); scape about twice as long as wide; flagellomere subquadrate, nearly as long as wide. Forewing relatively broad, length about 2.0× width of median part; costal space with eight subcostal veinlets on distal half; distal part of ScP curved posteriad; distal part of RA curved posteriad and connected with anteriorly curved RP, forming a loop; proximally RP+MA and MP not fused with each other; RP simple, with a ra-rp crossvein; MA simple, with a rp-ma crossvein; three or four crossveins present between RP+MA and MP; MP bifurcated; Cu branched near wing base; CuP proximally zig-zagged; two cua-cup crossveins present; three cup-a1 crossveins; A2 with a long, distally bifurcated anterior branch and a short, strongly curved posterior branch; two a1-a2 crossveins present; distal-most crossveins among longitudinal veins from RA to A2 arranged into a gradate series. Hind wing slightly narrower than forewing; costal space distally with a few subcostal veinlets; a short oblique stem of MA present near wing base; RP simple, distally slightly curved anteriad; MP and CuA separated by distinct membrane; distal-most crossveins among longitudinal veins from RA to CuA arranged into a gradate series. Abdominal plicatures present on segments 3–4.

Etymology. The generic epithet *Cretaconiopteryx* is a combination of *Creta-* (meaning Cretaceous) and *Coniopteryx* (a typical genus name of dustywings). The name is feminine.

Remarks. The new genus is distinguished from all other dustywing genera by the forewing RP+MA originated from R near wing base, the forewing RA and RP distally forming a loop, the proximally zig-zagged forewing CuP, the presence of 3–4 crossveins between forewing RP+MA and MP, the presence of crossveins between RP and MA and between MP1 and MP2, and the gradate-like arrangement of distal crossveins.

***Cretaconiopteryx grandis* sp. nov.** (Figs 1–3)

Diagnosis. Mostly as for the genus. The forewing with six distinct, ovoid, pigmented spots may be an important diagnostic character of the new species.

Description. Female. Body length 5.27 mm; integument dark brown, with abdomen slightly paler.

Head longer than wide, with prominent compound eyes; frons well-sclerotized between antennal insertions; gena elongated; vertex feebly domed. Antenna with scape stouter than pedicel and flagellomeres, scape distinctly longer than pedicel, pedicel about twice as long as wide; flagellomeres each subquadrate, nearly as long as wide, but terminal flagellomere bullet-shaped; flagellomeres with numerous, minute, suberect setae. Mouthparts chewing mandibulate; labrum subquadrate, anterolaterally rounded, and anteromedially slightly concaved; maxilla with galea segmented, terminal maxillary palpomere elongate elliptical, much longer and broader than preceding palpomeres; terminal labial palpomere elongate conical, much longer and broader than preceding palpomeres.

Prothorax slightly narrower than meso- and metathorax. Legs slender, with numerous, short setae; profemur nearly equal in length to mesofemur but shorter than metafemur, and slightly more swollen than meso- and metafemora; protibia shorter than meso- and metatibiae; tarsi 5-segmented; basitarsus longest tarsomere, about as long as combined lengths of remaining tarsomeres; tarsomere 4 apically expanded, marginally with a row of setae; pretarsal claws short, simple; arolium absent.

Forewing length 6.67 mm, maximal width 2.22 mm; membrane hyaline, slightly brownish throughout, with six distinct, ovoid, pigmented spots, respectively located at cells between RA and RP+MA, RP and MA, RP+MA and MP, MP1 and MP2, MP and CuA, and CuP and A1; an additional smaller spot present at distal cell between RP+MA and MP at least in

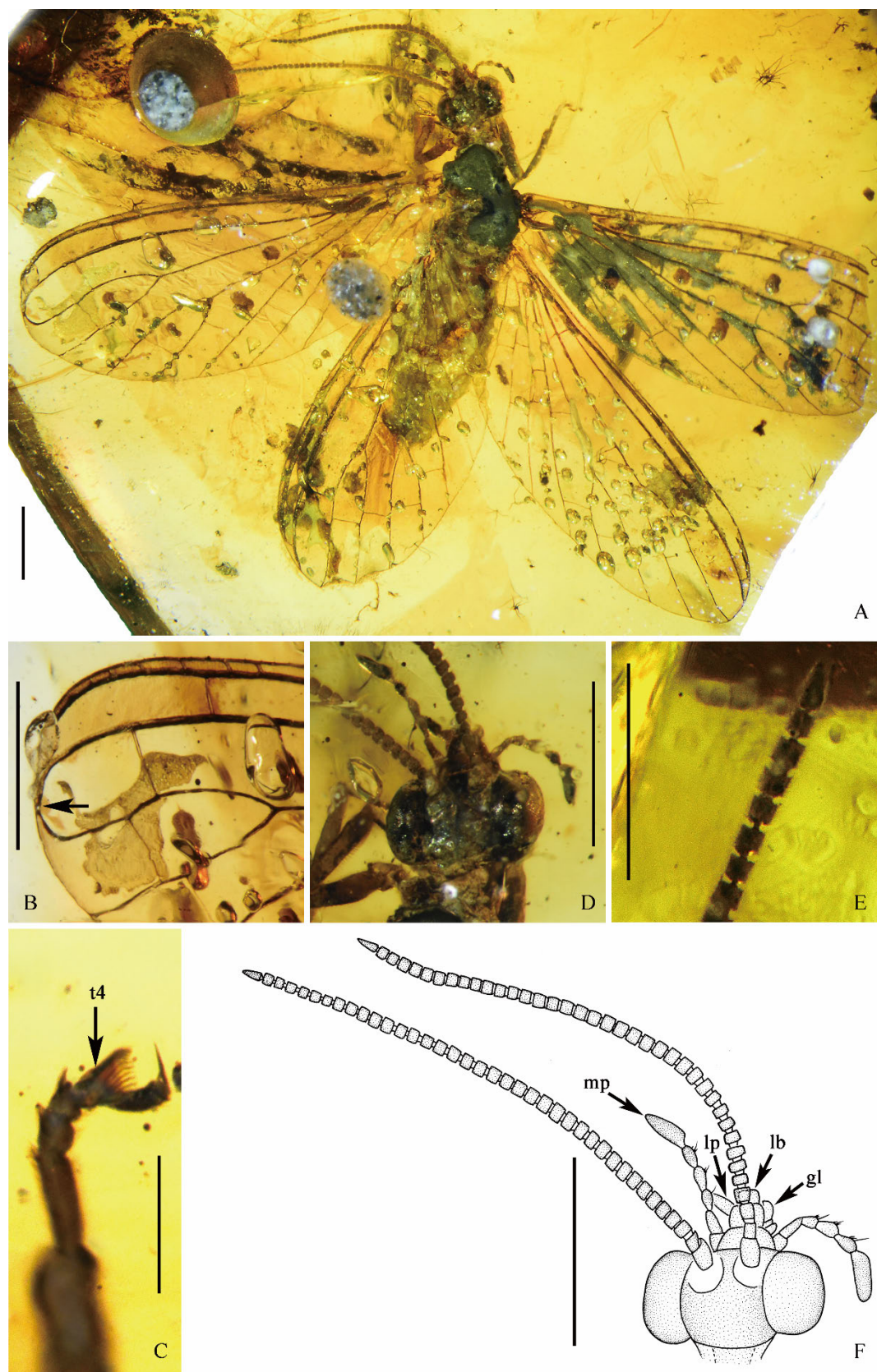


Figure 1. *Cretaconiapteryx grandis* **gen. & sp. nov.**, holotype female. A. Habitus photo, dorsal view. B. Photo of forewing apex, showing loop formed by RA and RP (indicated by an arrow). C. Photo of protarsus. D. Photo of head, dorsal view. E. Terminal segments of antenna. F. Drawing of head, dorsal view. Abbreviation: gl—galea; lb—labrum; lp—labial palp; mp—maxillary palp; t—tarsomere. Scale bars: A–B, D, F=1.0 mm; C=0.25 mm; E=0.5 mm.

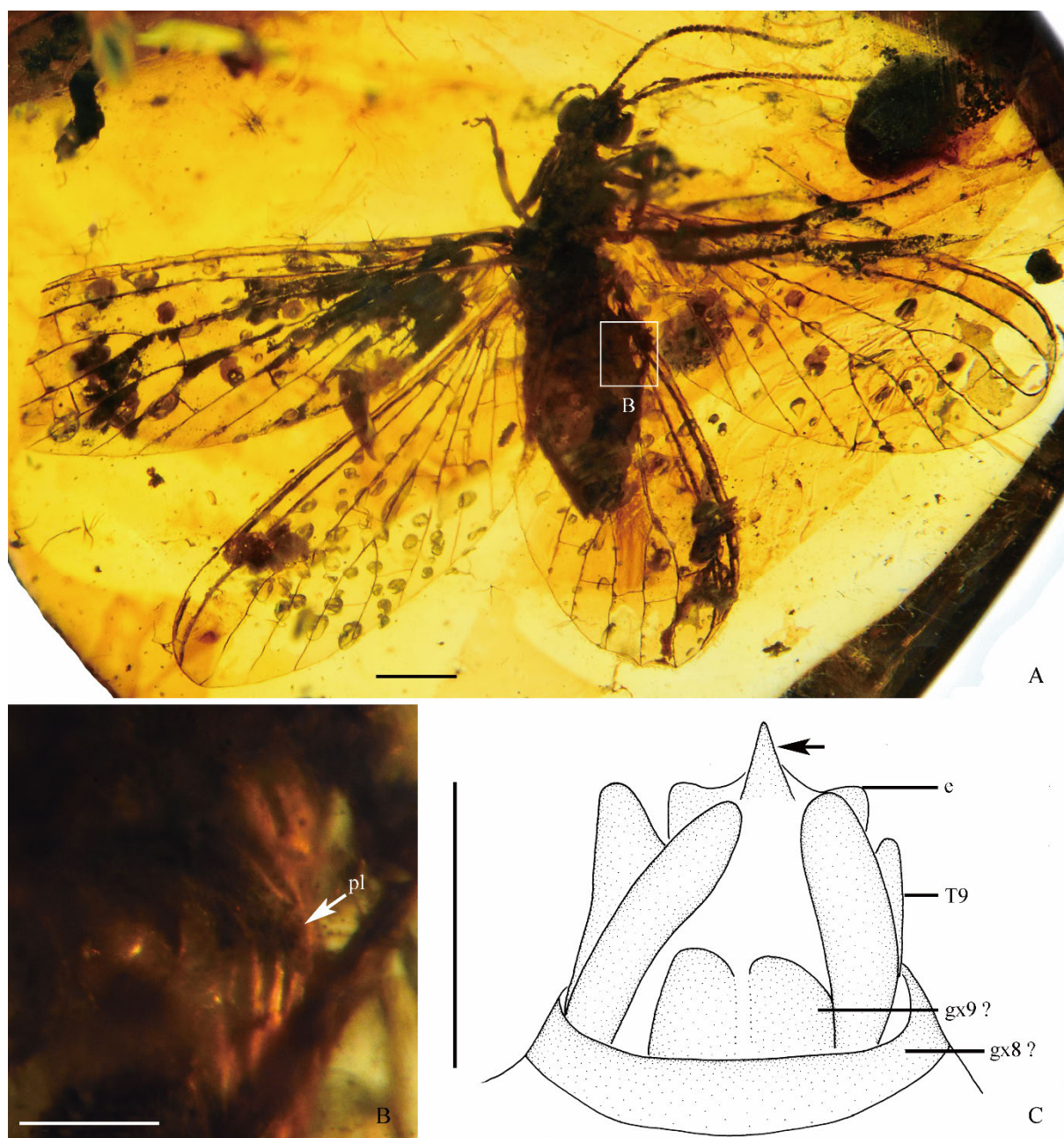


Figure 2. *Cretaconiopteryx grandis* gen. & sp. nov., holotype female. A. Habitus photo, ventral view. B. Lateral portion of abdominal segment 3 (as located on A) showing plicature (indicated by an arrow), ventral view. C. Drawing of genitalia (arrow indicated putative element of segment 10), ventral view. Abbreviation: e—ectoproct; gx—gonocoxite; pl—plicature; T—tergum. Scale bars: A, C = 1.0 mm; B = 0.5 mm.

left forewing; a short, simple, recurrent humeral veinlet present; costal space proximally with two costal crossveins, while also with eight subcostal veinlets on distal half; ScP largely parallel to costal margin, distally curved posteriad; one scp-ra present at distal 1/4 of subcostal space; RA distally curved posteriad and connected with anteriorly curved RP, forming a loop; one ra-rp present distad scp-ra; origin of RP+MA near wing base; RP simple, distally curved anteriad; MA simple and straight; one rp-ma present distad ra-rp; MP bifurcated at about distal 1/3; one r-mp, two or three rp+ma-mp, and one ma-mp present; one mp1-mp2 present; RP/MA fork and MP1/MP2 fork generally similar in shape and size; stem of M nearly touching Cu; Cu forked near wing base; CuA straight and simple; CuP simple, proximally zig-zagged; two cua-cup present; A1 simple; three cup-a1; A2 with a long, distally bifurcated anterior branch and a short, strongly curved posterior branch; two a1-a2 present; distal-most crossveins among longitudinal veins from RA to A2 arranged into a gradate series; marginal setae present, and those on hind margin much more widely spaced than those on costal margin.

Hind wing length 5.89 mm, maximal width 1.85 mm, similar to forewing, but immaculate; costal space distally with at

least four subcostal veinlets; ScP largely parallel to costal margin, terminally abruptly bending toward RA (or alternatively interpreted as connected by a crossvein with RA); RA distally feebly curved posteriad; one ra-rp+ma and one ra-rp present; origin of RP+MA near wing base; RP simple, distally feebly curved anteriad; MA simple and straight, a short oblique stem of MA present near wing base; one rp-ma present distad ra-rp; MP bifurcated at about distal 1/3; two rp+ma-mp, and one ma-mp present; one mp1-mp2 present; RP/MA fork and MP1/MP2 fork generally similar in shape, but the latter fork slightly smaller than the former one; stem of M nearly touching R; Cu forked near wing base; CuA and CuP both straight and simple; two closely spaced cua-cup present; A1 simple; two cup-a1; A2 distally bifurcated, with a short crossvein between stem of A2 and hind margin; distal-most crossveins among longitudinal veins from RA to CuA arranged into a gradate series; marginal setae present, and those on hind margin much more widely spaced than those on costal margin.

Abdomen large, broad, greatly tapering to narrow apical segments; plicatures present at least on segments 3–4. Genital structures only visible in ventral view; putative gonocoxites 8 fused as a short, transverse subgenital plate; tergum 9 broad, slightly prominent posteriad; gonocoxites 9 much shorter and narrower than tergum 9, slightly depressed medially; ectoproct short, with obtuse posterolateral corners; an acutely pointed sclerite present beneath ectoproct, possibly being part of segment 10.

Male. Unknown.

Material examined. Holotype. CAM BA-0008 (amber piece preserving a complete adult female of *C. grandis* **sp. nov.** and two midges; it is polished in the form of a nearly elliptical transparent cabochon, with length×width about 10.2×8.0 mm, height about 5.3 mm), Lowermost Cenomanian, Tanai Village, Hukawng Valley, northern Myanmar.

Etymology. The specific epithet *grandis* refers to the large body-size of the new species among known dustywings.

4 Discussion

4.1 Distinctive morphological characters of *Cretaconiopteryx* gen. nov.

The new dustywing genus has the largest body-size among all known fossil genera, with forewing length more than 6.5 mm, and it is also larger than all extant genera of Aleuropteryginae and Coniopteryginae that have the forewing no longer than 6.0 mm (Sziráki, 2011). The extant genus *Flintoconis* Sziráki, 2007 of the subfamily Brucheiserinae is the only dustywing genus larger than *Cretaconiopteryx* **gen. nov.**, with forewing length 8.5–9.2 mm (Sziráki, 2007).

The presence of a number of subcostal veinlets on distal part of costal space (Figs 1B, 3) is rarely found in Coniopterygidae and among other dustywings. It is only found in two extant species from South Africa, i.e., *Pseudoconis maculipennis* Meinander, 1972 (see Meinander, 1972: fig. 91F) and *Helicoconis (Capoconis) capensis* Enderlein, 1914 (see Meinander, 1972: fig. 76G).

The specialized feature of forewing RA and RP that are distally fused and form a loop (Figs 1B, 3) is very peculiar and has not yet been found in all other lacewing species. However, whether it is a diagnostic character for the new subfamily and new genus or just for the new species is still unknown.

The proximally zig-zagged forewing CuP (Fig. 3B) is also scarcely present in Coniopterygidae and other lacewing families. In the extant dustywing genus *Brucheiser* Navás, 1927 (Brucheiserinae), the wing veins are in general zig-zagged (Riek, 1975), but the proximal part of forewing CuP is not similarly modified to that in *Cretaconiopteryx* **gen. nov.**

The presence of 3–4 crossveins between forewing RP+MA and MP and the presence of crossvein between RP and MA in the new genus are only shared with *Brucheiser*. However, the involvement of these crossveins with other distal crossveins forming a gradate series is unique and only present in the new genus.

In addition, the branching condition of forewing A2 and the hindwing ScP abruptly terminated and curved posteriad toward RA by a short veinlet (Fig. 3) are of interest and have never been found in other dustywings.

4.2 Phylogenetic position of *Cretaconiopteryx* gen. nov.

The phylogeny within Coniopterygidae is lacking comprehensive study by modern approaches. The arguments for the subfamilial division and the intergeneric relationships within Aleuropteryginae and Coniopteryginae were discussed in Meinander (1972) but without any rigorous cladistics analysis. Zimmermann *et al.* (2009) provided a detailed morphological study on Coniopterygidae and proposed the subfamilial relationships, i.e., Aleuropteryginae + (Brucheiserinae + Coniopteryginae), based on larval morphology. A comprehensive analysis based on morphological and molecular data including both fossil and extant genera is crucial for understanding the evolutionary history of Coniopterygidae, but it is out of the scope of the present paper. Moreover, performing such phylogenetic analysis based on total-evidence data needs

morphological data of genitalia, which provide a number of phylogenetically informative characters, but in most fossil dustywing species these data are lacking.

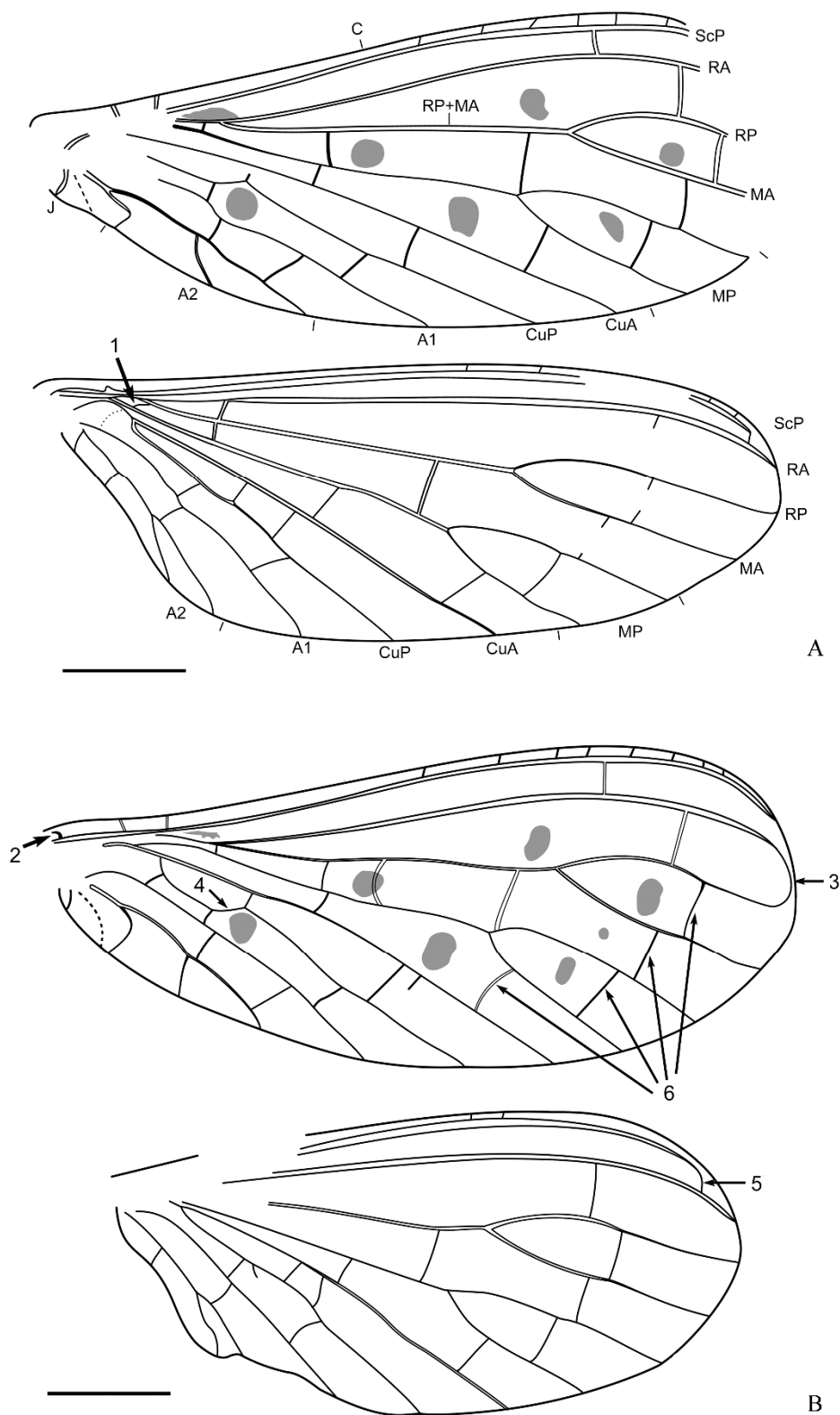


Figure 3. Drawings of fore- and hindwings of *Cretaconiopteryx grandis* **gen. & sp. nov.**, holotype female. A. Right fore- and hindwing; B. Left fore- and hindwing. Arrows: 1, stem of hind wing MA; 2, forewing humeral veinlet; 3, loop formed by forewing RA and RP; 4, zig-zagged proximal part of forewing CuP; 5, abrupt curve of hind wing ScP (or distal scp-ra crossvein); 6, gradate-like arrangement of distal crossveins. Scale bar = 1.0 mm.

Nevertheless, the tentative subfamilial affiliation of the new genus can be inferred based on the adult morphology. First, *Cretaconiopteryx* **gen. nov.** undoubtedly does not belong to Coniopteryginae by the segmented galea (Fig. 1F), the presence of 3–4 crossvein between forewing RP+MA and MP (Fig. 3), and the presence of plicatures (Fig. 2B). Lacking of these character states is probably autapomorphy of Coniopteryginae. Second, the new genus differs from Brucheiserinae by lacking the enlarged pronotum covering relatively short and small head, which is a putative autapomorphy of this peculiar subfamily.

The new genus shares with relatively more character states with Aleuropteryginae, such as the segmented galea, the presence of plicatures, and the hind wing RP+MA originated near wing base. The segmented galea is considered to be an apomorphic condition in Randolph *et al.* (2014), but this character state is present in most lacewings except for Sisyridae and two subfamilies of Coniopterygidae (i.e., Brucheiserinae and Coniopteryginae). Thus, it is hard to consider the segmented galea to be the autapomorphy of Aleuropteryginae, and in Meinander (1972) this character state is interpreted just as plesiomorphic. The presence of plicatures is considered to be apomorphic in Meinander (1972), but a contrary interpretation as plesiomorphic was proposed in Zimmermann *et al.* (2009). The relatively proximal origin of hindwing RP+MA is obviously plesiomorphic.

There are two apomorphic wing character states that at least support the monophyly of most Aleuropteryginae, i.e., the presence of stiff setae on stem of forewing MP and the closely spaced hind wing MP and CuA. The former character state is present in most aleuropterygines except *Aleuropteryx* and two fossil genera (*Glaesoconis* Meinander, 1975 and *Libanoconis* Engel, 2002), possibly being an autapomorphy of Aleuropteryginae if considering the absence of such stiff setae as secondary in these three genera. The latter character state is present in almost all extant aleuropterygine genera but absent in all Cretaceous genera as well as two extant genera (*Pseudoconis* Meinander, 1972 and *Vartiana* Aspöck & Aspöck, 1965). Among the aleuropterygine genera only two genera, i.e., *Glaesoconis* and *Libanoconis*, lacks both of the above character states, but they possess a peculiar, distally trifurcated forewing MP together with other two Cretaceous genera (*Apoglaesoconis* Grimaldi, 2000 and *Achlyconis* Engel, 2016). Engel (2016) mentioned that the three-branched MP is probably plesiomorphic. However, considering the presence of two-branched MP in all major lineages of dustywings, including the presently described new genus, the trifurcated MP could be in fact apomorphic and support the close relationships among these Cretaceous aleuropterygines that are placed in the tribe Fontenelleini. Hence, due to lack of the aforementioned distinctive apomorphic character states of Aleuropteryginae, there is no convincing argument to place *Cretaconiopteryx* **gen. nov.** into this subfamily as well. Moreover, considering the unique configuration of wing venation, such as the proximal origin of fore- and hindwing RP+MA, the forewing RA and RP distally forming a loop, the zig-zagged forewing CuP, and the gradate-like arrangement of distal crossveins, the erection of a new subfamily based on *Cretaconiopteryx* **gen. nov.** is justified. Putative autapomorphies of Cretaconiopteryginae **subfam. nov.** consist of the forewing RA and RP distally forming a loop, and the zig-zagged forewing CuP. Nonetheless, these peculiar characters might also be just autapomorphies of *Cretaconiopteryx* **gen. nov.** or even *C. grandis* **sp. nov.** Future findings of other taxa of Cretaconiopteryginae **subfam. nov.** could be helpful to further elucidate the phylogenetic status of this subfamily.

The reduction of wing venation seems to be the evolutionary trend of Coniopterygidae. This phenomenon might be correlated to the minimization of the dustywing body-size, although the relatively large-sized brucheiserine genus *Flintoconis* also has reduced wing venation (Sziráki, 2007). However, *Cretaconiopteryx* **gen. nov.**, by having relatively large body-size, shows some plesiomorphic wing character states, such as the denser crossvenation and the proximal origin of RP+MA in both fore- and hind wings. In addition, it possesses some other plesiomorphic character states, such as the segmented galea and the presence of plicatures. Consequently, the new genus as well as Cretaconiopteryginae **subfam. nov.** is likely to be the basalmost lineage among known dustywings and the sister group of the clade including all other three dustywing subfamilies. Thus, the monophylum comprising the three comparatively advanced dustywing subfamilies (i.e. Aleuropteryginae, Brucheiserinae and Coniopteryginae) might be supported by the apomorphic wing character states, specifically the distal origin of forewing RP and the reduction of crossveins.

5 Concluding remarks

The spectacular new dustywing genus *Cretaconiopteryx* **gen. nov.** from the mid-Cretaceous Burmese amber is of high significance for understanding the phylogeny and evolutionary history of Coniopterygidae. Being as a putative basalmost dustywing lineage, the new genus provides valuable evidence to interpret the evolutionary polarization of many morphological characters. Obviously, it is necessary to reconstruct the phylogenetic relationships within Coniopterygidae in future studies. Nonetheless, discovery of more fossil dustywings, particularly those phylogenetically significant groups as

the one herein reported, is desirable to elucidate the evolutionary history of Coniopterygidae.

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